Evaluation of Bioenergetics Models for Predicting
Great Blue Heron Consumption of Rainbow Trout at Hatcheries

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Abstract.—We predicted consumption of rainbow trout *Oncorhynchus mykiss* by great blue herons *Ardea herodias* by combining a population estimate of predators with bioenergetics models of (1) existence metabolism (ME), (2) existence metabolism plus reproductive costs ($ME_{Breeding}$), and (3) field metabolic rate (FM) for individual great blue herons. We then compared predicted consumption to directly estimated consumption by a free-ranging population of great blue herons foraging at a fish hatchery. Although the FM model predicted annual population consumption rates similar to observed annual consumption, model predictions differed significantly from directly estimated consumption for 6 months. Monthly consumption predicted by the existence metabolism models agreed with directly estimated consumption from October to June. During the breeding season (May–July), directly estimated consumption was higher than predicted by the ME model for nonbreeders but was lower than predicted by the $ME_{Breeding}$ model. This result would be expected if 20–30% of the great blue herons were reproductive. Peak population consumption was observed in August but was not predicted by the models. This discrepancy probably resulted from an influx of migrant great blue herons that were not detected during observations of population-level estimates. Model predictions would be improved most by using more reliable estimates of great blue heron abundance and by explicitly measuring the proportion of breeding birds in the population. Given accurate predator population estimates, bioenergetics models provide reliable, cost-effective estimates of fish losses to piscivorous birds.

Avian bioenergetics models have been used increasingly over the last 20 years to estimate energy flow between populations (Wiens and Scott 1975; Furness 1978; Weatherhead et al. 1982; Bernstein and Maxson 1985; Guillet and Furness 1985; Wood 1987a, 1987b; Birt-Friesen et al. 1989; Cairns et al. 1991; Madenjian and Gabrey 1995). The popularity of this approach results in part from a need for indirect assessments of the energy demands of populations. The parameters needed to estimate energy demand with bioenergetics models are easily determined in the laboratory, whereas field estimates of consumption are difficult.

Most avian bioenergetics models use interspecific allometric equations to estimate a species' metabolic energy demand under varying environmental conditions (Aschoff and Pohl 1970; Kendeigh 1970; Kendeigh et al. 1977; Nagy 1987).

Although many of the physiological variables used in bioenergetics models are now species specific (Masman and Klaassen 1987; Birt-Friesen et al. 1989), the validity of applying laboratory-derived measures of energy demand to field settings has been questioned (Weathers 1979; Nagy 1987; Ney 1993). Bioenergetic model predictions have only rarely been corroborated with independent data, and this has never been done in terrestrial systems (Ney 1993; but see fisheries papers Rice and Cochran 1984; Beauchamp et al. 1989). The energy estimates that bioenergetic models provide can vary widely depending on which model is applied. For example, estimates of energy demand from existence metabolism models can vary by up to 50% from field metabolic rate models that use doubly labeled water (Weathers et al. 1984; Williams and Nagy 1984). Existence metabolism is determined through feeding trials of caged birds that maintain a constant mass while they are exposed to variable ambient temperatures (0°C, 30°C; see

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Kendeigh 1977). Field metabolic rate is determined by comparing the fractional metabolic use of hydrogen and oxygen isotopes of birds in the field (^{3}H and ^{18}O respectively, see Nagy 1989). Estimated metabolism from both methods is plotted against bird mass to provide a mass–metabolism relationship that then can be used to determine the metabolism of other species with different masses. The fundamental differences between these models and a fish model are that birds are determinate growers, nestling care is costly to the parent (feeding offspring), and birds are endothermic. Typically, model validation involves comparison to other models rather than testing model predictions against observed energetic demand. For avian bioenergetics models to be credible, model predictions should be compared with independent estimates of energetic consumptive demands.

Estimating consumption by birds is of interest to fishery managers and ecologists because avian predation may have a significant impact on fish populations in natural and aquacultural settings (Furness 1978; Guillet and Furness 1985; Schramm et al. 1987; Wood 1987b; Madenjian and Gabrey 1995). Field studies of the impacts of mobile predators, such as birds, on fish in large systems are difficult and cost-prohibitive (Weatherhead et al. 1982; Barlow and Bock 1984; Parkhurst et al. 1992; Ney 1993; Pitt 1993). Fish hatcheries provide opportunities to test the ability of avian bioenergetics models to predict predation impacts on fish populations because the fish resources are quantified and located in discrete patches. Furthermore, reliable estimates of fish consumption by birds at fish hatcheries are needed to assess the cost-effectiveness of potential management practices to alleviate predation (Pitt and Conover 1996).

Our objectives were to develop and test the ability of three bioenergetics models to estimate avian population consumptive demand. We selected models that were readily available in the literature and were developed for nonpasserine birds. We then developed three models of consumption by combining a population estimate of predators with bioenergetics models of (1) existence metabolism (ME), (2) existence metabolism plus reproductive costs ($ME_{Breeding}$), and (3) field metabolic rate (FM) for individuals. We hypothesized that directly estimated consumption should equal existence metabolism for nonbreeding birds throughout the year. For breeding birds consumption should equal ME during the nonbreeding season

and existence metabolism plus reproductive costs during May–July ($ME_{Breeding}$ model). For comparison, we also provide alternative estimates of consumption based on field metabolic rate. We predicted consumption rates of fish by a population of great blue herons *Ardea herodias* at a Utah fish hatchery using models of ME, $ME_{Breeding}$, and FM, coupled with estimates of the hatchery great blue heron population size, diet composition, and body mass. We then tested the model predictions using an independent data set of observed great blue heron consumption of fish at this hatchery (Pitt and Conover 1996).

Study Site

Midway Fish Hatchery (MFH), administered by the Utah Division of Wildlife Resources (UDWR), is located in a mountain valley (elevation, 1,700 m; area, 625 km^2) approximately 60 km southeast of Salt Lake City (Pitt 1995). The region is high desert characterized by sagebrush *Artemesia* spp., very few trees, and few natural water sources. Surrounding land is used for small cattle operations with interspersed rural housing. Undeveloped lands include a river (with managed water flows), a large reservoir and park, and dry mountainous terrain in adjacent U.S. National Forest land. The reservoir was periodically stocked with rainbow trout *Oncorhynchus mykiss* (>30 cm), although a major portion of the fish in the reservoir are brown trout *Salmo trutta*. Foraging areas in the reservoir are limited due to high canyon walls, extreme water depth, and lack of fish in areas accessible to great blue herons. The river was not stocked with fish and was extremely low due to the filling of an upstream reservoir. The nearest great blue heron colony (3 nests) and natural foraging areas are located 50 km southwest of MFH at Utah Lake (UDWR, unpublished data).

The hatchery produced 85,176 kg of catchable (>30 cm total length) and a small amount of fingerling (<10 cm) rainbow trout in concrete and earthen raceways during 1993. Concrete raceways were located close (<100 m) to the hatchery buildings, whereas earthen raceways were located up to 1 km from buildings. Some raceways were covered with nylon mesh or wires to inhibit bird predation, and birds were occasionally shot by MFH personnel. Historically, MFH experienced higher rates of avian predation than the nine other UDWR hatcheries. Hatchery managers speculated that predation losses represented 15% of annual production at MFH based on the number of missing fish. However, from an intensive observational study

from 1993 through 1994, Pitt and Conover (1996) estimated these losses at 7.1% of annual production, with great blue herons accounting for 44% of the total losses to avian predation.

Model Construction

We developed three models (ME, $ME_{Breeding}$, and FM), each based on different assumptions of energy demand. These models were used to predict monthly fish consumption by the great blue heron population. We estimated individual energetic needs using interspecific allometric regressions for existence metabolism and field metabolic rates of nonpasserines (Kendeigh et al. 1977; Nagy 1987). Existence metabolism included the metabolizable energy (total ingested energy − waste) required for standard metabolism (sensu Kendeigh 1970), specific dynamic action, thermoregulation, and limited activity (e.g., activity of birds in confinement). Although the models in Kendeigh et al. (1977) have been shown to underestimate daily energy expenditure in some species (Birt-Friesen et al. 1989), we have no justification for including an a priori activity multiplier. Existence metabolism was calculated from observed energy consumption of captive animals exposed to variable thermal conditions (Kendeigh et al. 1977). During the breeding season, the additional cost of rearing young (adults regurgitate food to feed offspring) was determined by calculating daily growth and maintenance costs of nestlings over the entire development period (60 d). We assumed that all great blue herons were breeding because nonbreeding adult great blue herons has not been documented (Butler 1994). Although field data did not produce evidence for breeding birds foraging at the hatchery, the data was limited, and a small number of breeding birds may have gone undetected. Thus, we included a reproductive model in the analysis for comparison. Egg production costs were considered neglible for this species and were not included in model development (Madenjian and Gabrey 1995). Field metabolic rate was estimated from allometric equations based on metabolism of free-ranging nonpasserine birds measured with doubly-labeled water (Nagy 1987, 1989). Field metabolic rate includes reproduction, growth, and routine activity, plus costs associated with existence metabolism (Nagy 1987). Additional energy lost as unmetabolizable and indigestible products were accounted for with species-specific coefficients of waste losses (Bennett and Hart 1993).

We collected data at MFH on great blue heron abundance, body mass, and proportion of fish in the diet (see Field Methods). A t-test was used to test for seasonal differences (i.e., migration versus nonmigration periods) in bird mass and fat score (Zar 1984). Model estimates of individual energy demands of breeding and nonbreeding adults were then compared with fish consumption observed in a parallel study (Pitt and Conover 1996). We tested model predictions against directly estimated consumption rates for each month using a t-test (Zar 1984).

We estimated existence metabolism (ME_a) of adult great blue herons with the allometric equations of Kendeigh et al. (1977) for nonpasserines (converted to Système International Units):

$$ME_a = 24.719 W_a^{0.50} \qquad (1)$$

at 0°C, and

$$ME_a = 4.498 W_a^{0.67} \qquad (2)$$

at 30°C; ME_a is existence metabolism (kJ·bird^{-1}·d^{-1}) and W_a is the average mass of adult birds (g). We calculated mass-specific existence metabolism by using the mean body mass (2,068 g, SD = 44, $N = 17$) of great blue herons in our study in equations (1) and (2) and interpolating linearly through the temperature range (°C) because existence metabolism varies linearly with temperature (Kendeigh 1969; Kendeigh et al. 1977). The equation for ME_a between the end points calculated at 0° and 30°C was

$$ME_a = -12.51 \, T + 1,124.1, \qquad (3)$$

where T = temperature.

The mean monthly temperatures for Heber, Utah, were used to approximate the ambient temperature variation at MFH (Utah Climate Center 1992). The Heber station was located in the same valley, approximately 10 km north of MFH. The use of ambient temperature as opposed to operative temperature has little effect on nonpasserine bird metabolic demand (Cartar and Morrison 1997).

Great blue herons lay eggs in early April and incubate for an average of 27 d (Pratt 1970; McAloney 1973). We assumed that breeding adults cared for their young from May to July, that young fledge at 60 d of age, but that parental care continues for an additional 30 d (Werschkul et al. 1977; Quinney 1982; Butler 1992; Bennett 1993). Great blue herons averaged 2.3 fledglings per nest or 1.2 per adult (Pratt 1970; Werschkul et al. 1977; Quinney 1982; Forbes et al. 1985). We also assumed that breeding pairs would share equally in the energetic costs of raising young. Daily growth of nestlings was determined by averaging growth

rates of male and female nestlings and assuming the weight at fledging equalled mean adult mass (Quinney 1982; Bennett 1993):

$$W_{jd} = 2{,}068/(1 + 42.5e^{-0.17\,d}), \qquad (4)$$

fledgling mass (W_{jd}) in grams was determined as a function of days (d) since hatching. We estimated daily total energy requirements of nestlings (TER_j) by partitioning nestling mass into average individual mass, W_{jd} (g), and gain per day, G_{jd} (g/d). Average TER_j was determined every 10 d to remain consistent with Hurwitz et al. (1978):

$$TER_j = [ME_j \cdot W_{jd}^{0.67} + G_{jd} \cdot D_j] \cdot 10. \qquad (5)$$

We used the maintenance energy requirement (ME_j = 9.69 kJ·$W_j^{-0.67}$·d^{-1}) and energetic growth equivalent (D_j = 8.92 kJ·g^{-1}) from Bennett (1993). We computed monthly energetic demand for nestling care by summing the three TER_j per month. We estimated the additional energy requirements for breeding adults ($ME_{aBreeding}$) by adding TER_j values (birds regurgitate food for nestlings), multiplied by average number of fledglings produced per adult (F) to ME_a for May–July,

$$ME_{aBreeding} = ME_a \qquad (6a)$$

for nonbreeding season, and

$$ME_{aBreeding} = ME_a + \sum (TER_{jt} \cdot F) \qquad (6b)$$

for breeding season; t is the number of 10-d stanzas of nestling care.

We calculated field metabolic rate (FM, kJ·$bird^{-1}$·d) with the allometric equation of Nagy (1987) for nonpasserine birds:

$$FM = 4.797 W_a^{0.749}; \qquad (7)$$

W_a is mass (g) of the bird. Although existence metabolism varies linearly with temperature (Kendeigh 1969), field metabolic rate does not (Nagy 1987).

We determined energy consumptive demand of great blue herons by dividing monthly total energetic budgets by the metabolizable energy coefficient (MEC = 0.87) for great blue herons feeding on rainbow trout, which is similar to great blue herons feeding on other trout species (Bennett and Hart 1993). We assumed that MEC was equal for nestlings and adults (Sibbald 1978). Individual energetic consumption demand was converted from a prey mass basis by dividing energy demand by the energy content (EC_{RBT}) of rainbow trout, 7.32 kJ/g wet weight (Bennett and Hart 1993). Thus, three bioenergetics based estimates of fish consumption (g·$individual^{-1}$·d^{-1}) by great blue herons were computed:

$$ME \text{ (nonbreeding)} = ME_a \cdot MEC^{-1} \cdot EC_{RBT}^{-1}; \quad (8)$$

$$ME \text{ (breeding)} = (ME_a + F \cdot TER_j)$$
$$\cdot MEC^{-1} \cdot EC_{RBT}^{-1}; \qquad (9)$$

$$FM = FM \cdot MEC^{-1} \cdot EC_{RBT}^{-1}. \qquad (10)$$

Field Methods

We compared the bioenergetics model predictions of fish consumption for breeding and nonbreeding birds to observed fish consumption as reported by Pitt and Conover (1996). Directly estimated consumption was presented as fish biomass consumed by the population of great blue herons foraging at MFH (Pitt and Conover 1996). We multiplied our bioenergetics model predictions by great blue heron monthly population size estimates to convert individual consumption rates to population-level rates for comparison with directly estimated consumption. Directly estimated consumption was determined by multiplying number great blue heron foraging hours per month by average consumption rate per foraging hour. We determined the number of birds foraging by scanning the hatchery hourly (hourly scans) within randomly selected 24-h sessions and averaging replicate scans for each hour on a per month basis. Consumption rate per foraging hour was determined by observing randomly selected birds that were foraging for up to 20 min (individual observations) and recording the number and length of fish consumed. Fish mass was determined from hatchery data by means of allometric mass–length relationships. See Pitt and Conover (1996) for further details on directly estimated consumption estimates and great blue heron behavior.

We conducted three 24-h sessions (96 scans) per month during April–September, and single monthly sessions (24 scans) during October–March from May 1993 to August 1994. During each hour of every session, we drove from one end of MFH to the other and counted all great blue herons in the area to determine their abundance and activity (Altmann 1974; Ralph 1981); we used a 407,600-cd spotlight at night. For each month, we used the highest count of great blue herons as the population size. Maximum counts can either underestimate populations, if all individuals are not visible at one time, or overestimate populations, if individuals from adjacent populations are counted. Because the maximum counts were usually consistent

over time and were verified with individual observations, they represent an adequate estimate of the population size, whereas average counts or the number of foraging birds would underestimate the population size. Model predictions of total daily consumption by individuals were multiplied by the maximum count each month to determine mean daily consumption for the great blue heron population foraging at MFH.

To evaluate the accuracy of population estimates during months (July–August) when great blue herons were difficult to observe, we compared the population estimates with the predicted number of birds determined by using the total number of hours birds were foraging. We determined the average number of foraging hours per bird in winter and used this to predict the great blue heron population throughout the year by dividing total daily foraging hours by the mean daily foraging hours per individual. For example, if we assume there is no change in the number of foraging hours per bird, then the number of foraging hours should correlate linearly with population estimates. By determining individual energy demand from population energy demand, individual energy demand can be examined to determine if changes are justified or values are within a realistic range (Whittow 1986).

In addition to our hourly scans, we observed birds from six different blinds for over 1,300 h to determine consumption rates, foraging hours per individual, movement behavior, and to test the reliability of population estimates derived from hourly scans (see Pitt and Conover 1996). The birds were tracked throughout 24-h periods, and individual birds were easily recognized during most of the year because individuals were observed continuously for up to 24 h. In addition, birds tended to display consistent behavior (e.g., rest on a particular tree limb, fly to a spot along a particular raceway to forage, then return to the same tree limb). We recorded data on activity (e.g., foraging, resting, flying) and breeding status as evidenced by plumage. Because of the sparse vegetation, we were able to view all birds continuously throughout the day whether they were feeding at MFH or in nearby fields (<300 m).

To determine if birds were feeding elsewhere or breeding, we searched local reservoirs and rivers for foraging great blue herons and their nests weekly from April through September and monthly from October through March. We observed one instance of a great blue heron foraging near the reservoir and one great blue heron nest near the

river within the valley. That nest was attended only during 1993, and no nestlings were observed. Less than 20% of the great blue herons observed were in breeding plumage, and most of these were observed before or after the breeding season.

We performed necropsies on all ($N = 17$) great blue herons shot by MFH personnel throughout the year and recorded bird mass, fat score, age-class, reproductive condition, and type and mass (wet weight) of crop contents. We used this information to determine breeding status and diet composition (e.g., hatchery rainbow trout versus reservoir brown trout). Crop contents were identified to the lowest taxonomic level possible (i.e., species for fish, family for insects, etc.). Rainbow trout could be easily distinguished from brown trout from the reservoir. Fat scoring was used to indicate general condition because poor condition might restrict reproduction. Fat scores were assigned on a scale of 0–5, according to Pitt (1995) modified from McCabe (1943), and Helms and Drury (1960).

Results

Field Observations

Average bird mass was 2,068 g (SE = 44, $N = 17$), with an average fat score of 2.4 out of 5 (SE = 0.3, $N = 17$). During August and September, average bird mass (1,958 g, SE = 23, $N = 6$) and average fat score (1.7, SE = 0.5, $N = 6$) were significantly less ($t = 2.00$, df = 17, $P = 0.03$ and $t = 2.14$, df = 17, $P = 0.02$, respectively) than for birds shot during the rest of the year (mean bird mass = $2,082 \pm 85$ g, $N = 11$ and mean fat score = 2.8 ± 0.4, $N = 11$). This difference may indicate that birds in poorer condition (e.g., reproductive birds) were cycling through the MFH area in addition to the birds that were in residence year round. The percentage of rainbow trout in the diet was 92% ($N = 17$) calculated from crop contents on a wet weight basis. All fish in crops were rainbow trout and had morphology consistent with hatchery fish (i.e., size and fin wear). The remaining 8% was unidentifiable remains (plants, animal matter, and inorganic substances) and some insect larvae (primarily Odonata). However, to provide an upper bound for our models, we assumed that 100% of the energy was coming from MFH fish.

The maximum number of great blue herons observed at MFH remained consistent over hours and days. Thus, the maximum number observed approximated the mean number of birds present at MFH for much of the year. However, all birds did
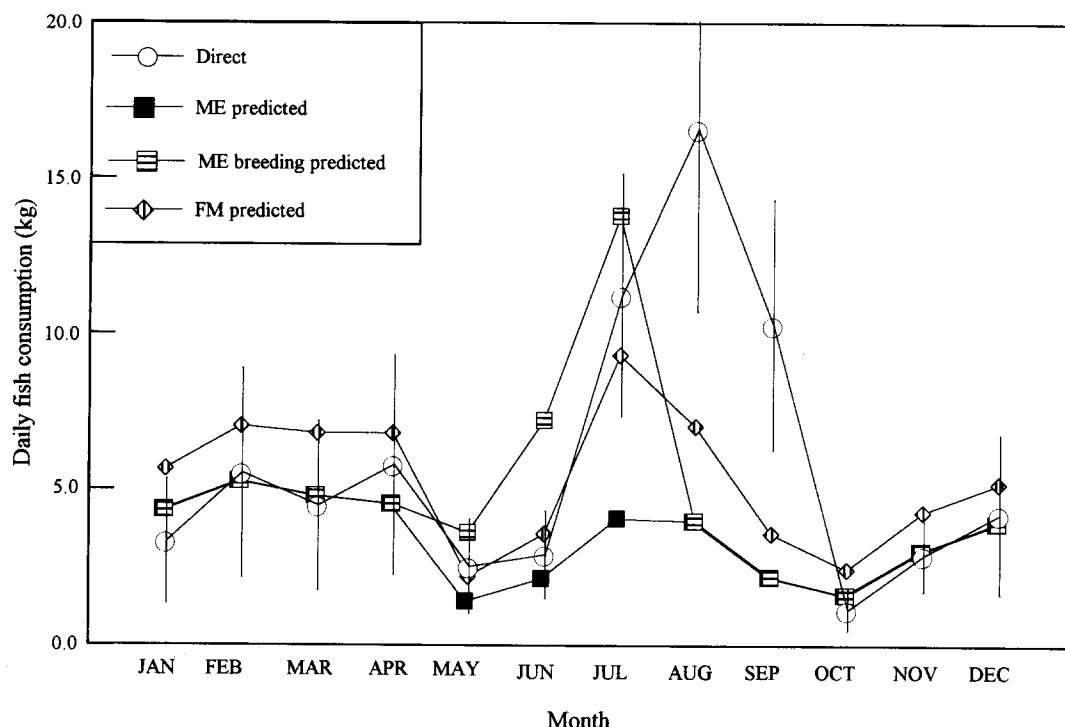
FIGURE 1.—Mean daily fish consumption by a local population of great blue herons, as predicted from bioenergetics models of existence metabolism for average breeding (ME breeding) and nonbreeding (ME) great blue herons, bioenergetics model of field metabolic rate (FM), and as determined by direct estimation at Midway Fish Hatchery in Utah (Pitt and Conover 1996). Error bars represent 95% confidence intervals.

not forage at once. While some birds flew to raceways to forage, others remained in fields and trees adjacent to MFH. During most of the year, all birds could be followed throughout the day because they remained at MFH continuously.

Individual Consumption

The ME model for nonbreeding great blue herons predicted that daily consumption of hatchery rainbow trout by the individual great blue herons ranged from 127 g/d in July to 174 g/d in January. Consumption predicted from the ME$_{Breeding}$ model was 363 g/d in May, 451g/d in June, and 431 g/d in July. Consumption predicted from FM was 229 g/d.

Modeled Population-Level Consumption

Monthly changes in consumption predicted from both the breeding and nonbreeding ME models were due in part to changes in great blue heron population size and to changes in thermoregulatory costs associated with temperature (mean monthly temperature range: −6.0°C in January to 19.7°C in July; Utah Climate Center 1992). In ad-

dition, daily consumption predicted for breeding great blue herons varied with ontogenetic changes in nestling energy requirements. Each nestling consumed an estimated average 183 g/d, 264 g/d, 253 g/d for May, June, and July, respectively. Reproduction was predicted to increase consumption by a factor of 1.5–2.4 over that of nonbreeding great blue herons during May–July. In contrast, monthly changes in field metabolic rate predictions were due solely to changes in great blue heron population size. Observed population-level daily consumption rates (Pitt and Conover 1996) ranged from 1.1 kg to 5.72 kg for October–May, increased slightly during the breeding season, and peaked during August at 16.5 kg (Figure 1).

Comparison of Bioenergetics Model Estimates to Directly Estimated Consumption

Predictions from all three population-level models showed good agreement with the directly estimated consumption rate in 6–9 months out of the year. The largest deviations from directly estimated consumption occurred during July–September (Figure 1). Consumptive demand predicted by
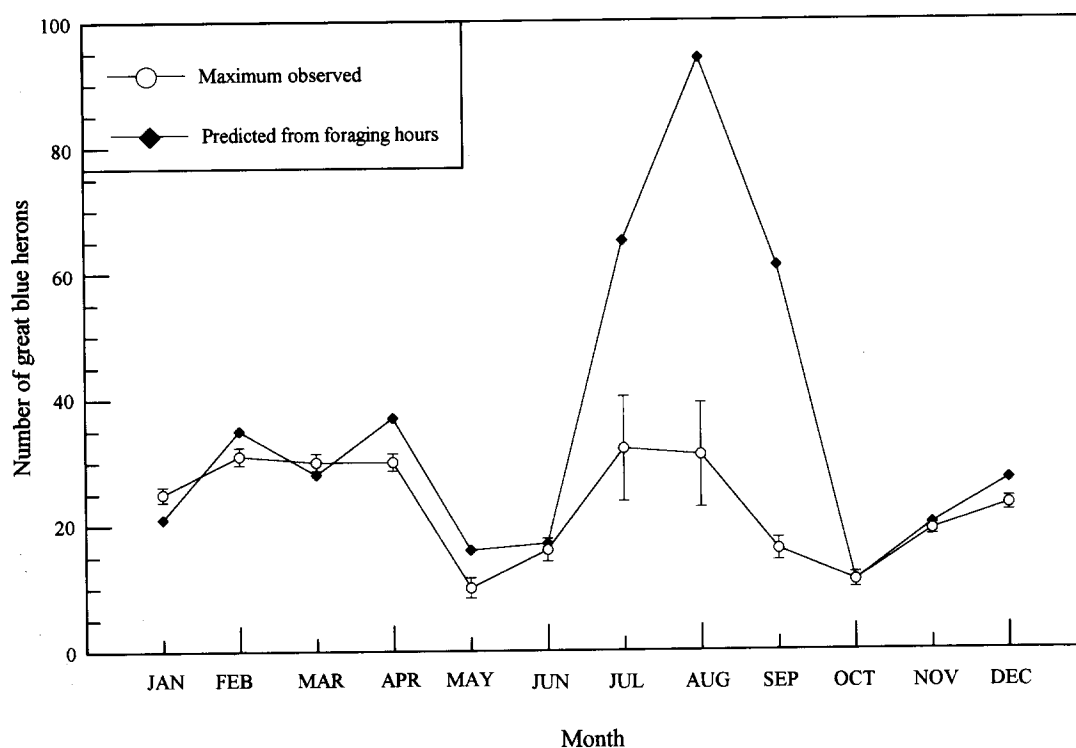
FIGURE 2.—Numbers of great blue herons visiting the Midway Fish Hatchery in Utah based on the maximum number of herons observed each month and as computed from monthly means of total population foraging hours per day and foraging hours per heron in winter. Error bars represent ± SD.

ME for nonbreeding great blue herons did not differ significantly ($P > 0.05$) from the consumption rate observed by Pitt and Conover (1996) for 9 months of the year, from October–June (Figure 1). During this period, monthly population consumption rates predicted from the ME model averaged 3.46 kg/d, compared with a mean directly estimated consumption rate of 3.58 kg/d. However, during July–September, directly estimated consumption rates were significantly higher ($P < 0.05$) than predictions from the ME model for a nonbreeding population. Consumptive demand predicted by $ME_{Breeding}$ ($ME = ME_{Breeding}$ during nonbreeding season) did not differ significantly ($P > 0.05$) from the consumption rate observed by Pitt and Conover (1996) for 9 months of the year (October–May, July). During the breeding season (May–July), the $ME_{Breeding}$ model overestimated observed population-level consumption. Consumption predicted from the field metabolic rate model did not differ significantly ($P < 0.05$) from directly estimated consumption for 6 months of the year (December and February–June). Although predicted consumption demand for the two exis-

tence metabolism models tracked temporal changes in directly estimated consumption more closely than the FM model, annual population-level consumption estimates from ME model (1,257 kg) and from $ME_{Breeding}$ model (1,778 kg) differed significantly ($P < 0.05$) from observed population-level annual consumptive demand (2,138 kg, SE = 162). Annual consumption predicted from the field metabolic rate model (1,972 kg) was similar to observed population consumption.

Discrepancies between directly estimated and predicted consumption were probably caused in part by temporal changes in great blue heron abundance and the accuracy of population estimates. Population estimates ranged from 10 to 32 individuals over the entire year (Figure 2). The population varied little (23–30) from December to April and remained low during breeding until July. Estimates were most variable from the end of the breeding season (July) into autumn.

Higher variability in estimated great blue heron abundance from July into autumn coincided with temporal changes in foraging patterns that were influenced by disturbance from hatchery workers.
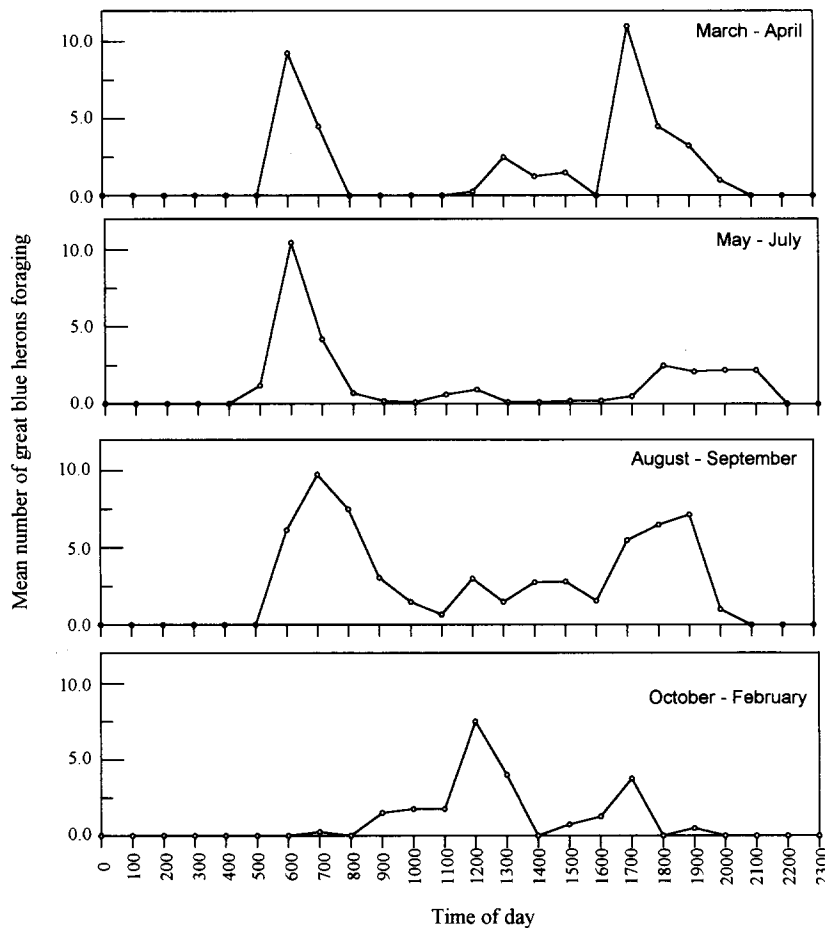
FIGURE 3.—Mean numbers of great blue herons foraging hourly during spring migration (March–April), summer (May–July), fall migration (August–September), and winter (October–February) at Midway Fish Hatchery in Utah.

During spring and early summer, most great blue herons foraged in daylight before and after working hours (0800–1630 hours) when MFH personnel were absent for an average of 7 h/d (Figure 3). However, during August and September, great blue herons foraged throughout the day in addition to morning and evening, averaging 13 h/d. Great blue heron foraging activity peaked at midday in winter, because MFH workers arrived before dawn and spent little time outside during the day. Great blue herons remained close to MFH throughout most of the year. Great blue herons were not observed moving to or from other areas during fall–spring, and individuals were easily recognized. During July–August, most great blue herons remained in the vicinity (<300 m) of MFH; however, additional individuals were observed going to and coming from other areas and may not have been

adequately accounted for in our abundance estimates.

During winter, foraging time ranged from 0.8 to 1.2 h per great blue heron, depending on foraging location. Foraging hours per bird were lowest after fish were removed from earthen raceways and confined to steep-sided concrete raceways. Population size predicted from total foraging hours closely paralleled the maximum counts from October to June; however, maximum counts were 49–74% lower than the population size predicted from total foraging hours from July to August (Figure 2).

Discussion

Individual Consumption

The individual consumption rates we predicted were lower than some reported in other studies

(Schramm et al. 1987; Bennett 1993), but much of the difference can be explained by the smaller body mass of resident birds in Utah (Dunning 1993). Using Kendeigh's (1970) allometric equations for existence metabolism, Schramm et al. (1987) estimated nonbreeding great blue herons would consume 300–340 g·individual^{-1}·d^{-1} in Florida compared with our estimates of 127–229 g·individual^{-1}·d^{-1} (ME–FM). This difference was due to 68% larger mean body mass of Florida great blue herons (3,175 g; Schramm et al. 1987). We estimated mean body mass by weighing birds shot at MFH, whereas Schramm et al. (1987) used mass data obtained from the literature and specimens in a Florida museum. This difference in mass may reflect size variation in great blue heron subspecies (Bent 1963). Schramm et al. (1987) also increased existence metabolism by 50% because the total energy requirement of free-ranging ciconiiformes were estimated previously at 1.5 times existence metabolism (Kahl 1964; Kushlan 1977). However, our results do not support the use of a high activity rate multiplier for free-ranging great blue heron existence metabolism at fish hatcheries. If we had applied a similar correction factor, our consumption estimates predicted from existence metabolism would have differed significantly from the directly estimated consumption for 7 months of the year. Our results suggest that a lower activity rate multiplier (1.2) may be more appropriate. Bennett (1993) estimated maintenance energy requirements of great blue herons in British Columbia at 1,434 kJ/d (196 g/d) for temperatures above 7.9°C (lower critical temperature). Gross energy intake ranged from 1,200 to 1,800 kJ/d, with this variation due, in part, to changing body mass (2,200–2,850 g) of cyclic fat storage and use. Bennett's (1993) great blue herons were held in large pens and aviaries (3.7 m × 5 m × 2.1 m in year 1 and 100 m × 50 m × 3 m in year 2), which allowed for a reasonable approximation of unconstrained routine activity. His estimated daily consumption rate was roughly 8% of adult body mass (Bennett 1993), which is similar to our existence metabolism estimates of daily consumption (6–8% of adult mass) for nonbreeding great blue herons.

Population-Level Consumption

Our existence metabolism model for nonbreeding great blue herons was a good estimator of free-ranging great blue heron consumption of fish at MFH for 9 months of the year. Directly estimated consumption rates fell between consumptive demands required for breeding and nonbreeding adult great blue herons and corresponded to a population of 25% breeders and 75% nonbreeders. Although close agreement between the directly estimated and predicted consumption rates does not validate the ME bioenergetics model, it does increase our confidence in the ability of bioenergetics-based models to estimate fish consumption. Monthly deviations from directly estimated consumption by the bioenergetic model predictions probably resulted more from inaccuracies in great blue heron abundance estimates than from inaccuracies in model estimates. Bioenergetic analyses of predation losses in fish populations are established and are more sensitive to errors in estimates of predator abundance than to errors in physiological parameters (Kitchell et al. 1977; Stewart et al. 1981, 1983; Hewett and Johnson 1992).

Although annual consumption predicted by field metabolic rate did not differ significantly from annual directly estimated consumption, the FM model did not track major temporal variations in consumption. Temporal variation of predation loss is important at fish hatcheries because the number of fish lost may be more economically relevant than the mass of fish removed (Parkhurst et al. 1992). For example, although only small amount of small (<10 cm) fish biomass is lost, the number of fish may be critical. During winter, only a small biomass of small (<10 cm) fish were lost, but the number of fish lost approximated the number lost during summer when a large biomass of large (>25 cm) fish were lost (Figure 4). The high number of fish lost during initial development translates into fewer fish available for stocking operations the following year. Thus, a model that tracks the monthly variation in predation losses may be valuable. Annual predictions from the FM model were more similar than the two ME models to the annual direct estimates of consumption. However, the field metabolic rate model underestimated directly estimated consumption during the summer, which was then compensated for by overestimating energy consumptive demand during the rest of the year. If we assume that the population estimates for July–September were inaccurate and exclude these months from the analysis, the annual consumption (973 ± 104 kg) agreed with annual population consumptive demand predicted from either existence metabolism model (nonbreeding: 940 kg, breeding: 1,160 kg) but differed significantly from the field metabolic rate predictions (1,349 kg). Field metabolic rate does, however, include premigratory costs that may be incurred during August and September.
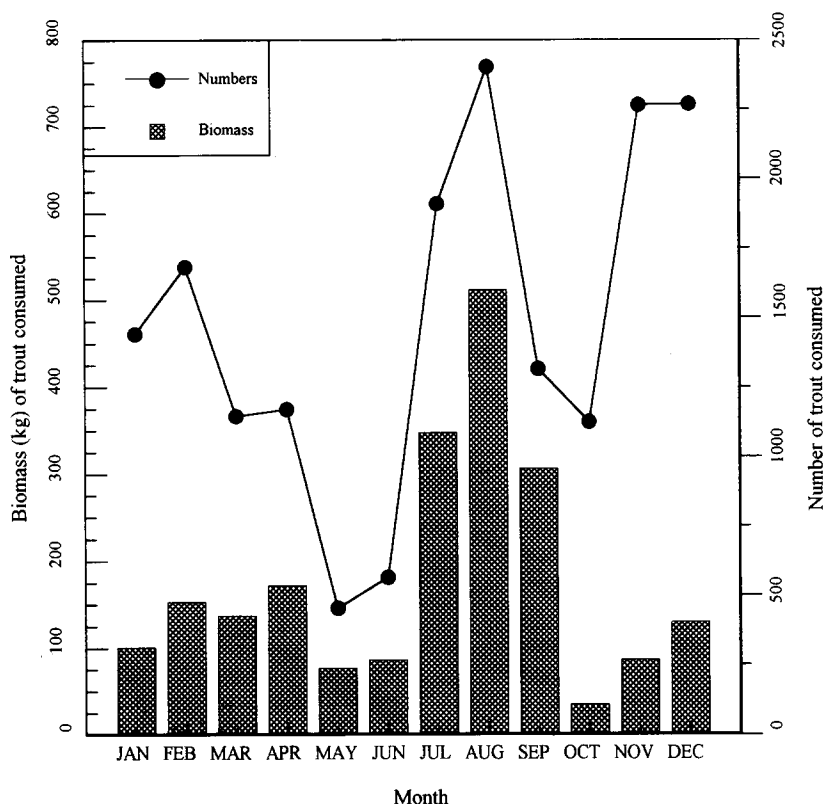
FIGURE 4.—Number and biomass (kg) of fish consumed monthly by great blue herons at Midway Fish Hatchery in Utah (Pitt and Conover 1996).

Differences between direct estimates of consumption by Pitt and Conover (1996) and our model-based predictions during the breeding season may have also resulted from a mix of breeding and nonbreeding birds foraging at MFH. We would expect the observed consumptive demand to fall between the nonbreeding and breeding consumptive demand predicted from existence metabolism during the breeding season (May–July). If only 25% of the great blue heron population was actually breeding, then consumptive demand predicted by the existence metabolism model would equal the directly estimated consumption rate. This predicted percentage of breeders in the population is lower than reported for songbirds, where an estimated 30–60% of the population was breeding (Smith 1978; Ollason and Dunnet 1988; Dhondt et al. 1989), but the percent of nonbreeding adult great blue herons has not been documented (Butler 1994). Birds might not have been reproductive because they were juveniles, lacked suitable nest sites, or attempted to nest but failed (Sternberg

1972; Ollason and Dunnet 1988; Madenjian and Gabrey 1995).

We found no evidence of breeding birds foraging at MFH. During nesting season, we did not observe birds in breeding plumage foraging at MFH; birds shot during this time were not in breeding condition; active nests were not found even though extensive searches were made within 50 km of MFH; and the decline in the number of birds foraging at MFH during April–June suggest that birds were nesting and foraging at an area much further from MFH. Moreover, colonies are not known to exist in the area, although UDWR and the Audubon Society has searched for and kept records of great blue heron colonies for many years (UDWR, unpublished data). Nonetheless, we may have underestimated the great blue heron population during the breeding season (May–July); breeding birds may have a lower probability of being observed because one adult may feed while the other attends the nest (Pratt 1970). Further, casual observations of plumage characteristics,

bird behavior, and a small necropsy sample is not definitive evidence that birds were not breeding.

We were most confident of our population estimates from October–March, when vegetation did not obstruct viewing and birds remained close to MFH throughout the day. Although maximum counts can underestimate the number of birds because the entire population may not be visible at one time, we observed the same number of birds consistently each hour and over several days. Further, we were able to track the birds for 24-h periods and they did not leave the immediate vicinity of MFH. Our model-based consumption estimates more closely approximated directly estimated consumption during this period. During August and September, directly estimated consumption diverged from predicted consumption, and this corresponded with a similar divergence between population estimates based on maximum counts versus those based on total foraging hours (Figures 2, 3). Furthermore, we asked hatchery workers to count the number of great blue herons they observed. During August and September, the number they reported fluctuated daily but was fairly consistent during the rest of the year.

Differences between directly estimated and predicted consumption rates for August and September could have also resulted from changes in energetic needs during this time of year, which were not accounted for in the two ME models. Most great blue herons in Utah migrate before October (Behle and Perry 1975). The decline in bird number during October suggests that some birds were migrating. Premigratory birds undergo increased energy needs due to fattening, muscle hypertrophy, increased body mass, and molting (Bent 1963; Blem 1976; Kendeigh et al. 1977; Hennemann 1983; Marsh 1984; Bennett 1993). Molting may increase basal metabolic rate by 26–46% and account for 8% of daily energy expenditure (Whittow 1986). Fat storage may also increase energy demand by up to 13% and increase body mass by 50% (Whittow 1986). Bennett's (1993) great blue herons increased their mass by 650 g from August to December. If we assume a similar increase (10.7 g/d from August to September) occurred in our study during August and September and also assume that this mass increase was due solely to lipid deposition (cost = 65.5 kJ/g lipid; Whittow 1986), the increased consumption (7.9 kg/d in August and 4.2 kg/d in September) still would not account for that observed by Pitt and Conover (1996; 16.5 kg/d and 10.2 kg/d in August and September, respectively). Additionally, our necropsy data, although

limited, did not support increases in mass or lipid deposition. Further, birds tend to lose energy reserves during molt, and energy intake normally peaks during winter (Kendeigh et al. 1977; Whittow 1986; Blem 1990; Bennett 1993).

Flocks of juvenile and migrating birds are transitory and might have caused inaccuracies in population size estimates during August and September, resulting in underestimates of model-based consumption estimates (Eckman 1981; Matthysen 1993). Migrating birds might have used MFH as a staging area, foraging for a few hours and then leaving. If so, our estimates of the population size based on maximum number seen during any hour would be too low.

Although fish predation has been perceived as an economic problem for more than 300 years, little progress has been made in quantifying bird depredation (Mills 1967; Draulans 1987). Fisheries biologists and managers need reliable estimates of such losses to decide whether control efforts are cost-efficient. Historically, hatchery managers have relied upon their own perceptions of loss to make these determinations. These are usually obtained from casual observations of bird activity or merely from differences between the starting and ending numbers of fish in raceways. Not surprisingly, these perceptions are often inaccurate (McIvor and Conover 1994; Pitt and Conover 1996). Bioenergetics models provide a reasonably accurate and economical means to estimate fish consumption by individual great blue herons at fish hatcheries. If observations by hatchery personnel can provide accurate estimates of great blue herons visiting MFH, then total losses from the great blue heron population can also be estimated. Thus, bioenergetics modeling can be used by hatchery managers to estimate losses with reasonable accuracy and to determine if potential reduction measures are economically justifiable.

Our results support the use of avian bioenergetics models to estimate consumption of hatchery fish by birds. Bioenergetics models are more cost-effective than long-term behavioral studies and are certainly more accurate than casual loss estimates perceived by managers (Pitt and Conover 1996). More sophisticated models that explicitly partition energetic costs (e.g., basal metabolism, thermoregulation, voluntary activity, egg production, fledgling rearing, and somatic growth) may yield more accurate results, but the burden of accurately estimating additional variables for a marginal increase in accuracy may not be warranted (Bartell et al. 1986). The accuracy of our relatively simple

models could be improved with better estimates of population size and structure, which are often easy to obtain. The sensitivity of model predictions to perturbations of an individual variable has been investigated thoroughly (for FM model see Nagy 1987, 1989; for ME see Kendeigh 1977; Madenjian and Gabrey 1995). From these analyses, the FM and ME models should be most sensitive to changes in the proportion of fish in the diet, which would also influence assimilation efficiency (Madenjian and Gabrey 1995). These models may be applied to other settings if the population structure, percentage of fish in diet, and activity costs can be quantified.

Acknowledgments

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